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On a stoichiometric two predators on one prey discrete model

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Abstract

In this letter, we first propose a discrete analogue of a continuous time predator–prey system, which models the dynamics of two predators on one prey [I. Loladze, Y. Kuang, J. Elser, W.F. Fagan, Competition and stoichiometry: Coexistence of two predators on one prey, Theor. Popul. Biol. 65 (2004) 1–15]. Then, we study the dynamics of this discrete model. We establish results on boundedness and global attractivity. Finally, several numerical simulations are given to support the theoretical results.

Keywords: Stoichiometry; Discrete model; Predator–prey model; Boundedness; Global attractivity

1. Introduction

The dynamic relationship between predators and their prey has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology. A traditional Lotka–Volterra type predator–prey model has received great attention, and has been well studied (see, e.g., [3–11] and references therein). Most recently, Sterner and Elser have expanded Lotka's vision to develop the field of ecological stoichiometry. Loladze et al. [1] discussed the dynamics of a stoichiometric continuous time producer–grazer system. Loladze et al. [2], by capturing the critical elements of ecological stoichiometry, constructed the simplest model for two predators on one prey, and analyzed competition between two predators on one prey, and showed that a stable equilibrium was possible with two predators on this single prey. We note that most existing models exhibiting these effects are continuous in time. However, in experiments, data are collected on discrete time intervals and many producers in nature have non-overlapping generations. Motivated by these considerations we shall analyze the dynamics of a discrete analogue of the continuous model in [2] with its discrete analogue in this letter. In the next section, we shall propose a discrete analogue of system (2.1). In Section 3, we shall establish easily verifiable sufficient criteria for the boundedness of solutions. Finally, a global attractivity result is obtained and some numerical simulations are presented to support these results.

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2. Discrete analogue of the model

Our discrete stoichiometric two predators on one prey model is based on the following continuous time predator–prey system due to Loladze et al. [2]:

$$\begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}t} = rx\left[1 - \dfrac{x}{\min(k, (p - s_1y_1 - s_2y_2)/q)}\right] - f_1(x)y_1 - f_2(x)y_2, \\ \dfrac{\mathrm{d}y_1}{\mathrm{d}t} = e_1 \min\left(1, \dfrac{(p - s_1y_1 - s_2y_2)/x}{s_1}\right) f_1(x)y_1 - d_1y_1, \\ \dfrac{\mathrm{d}y_2}{\mathrm{d}t} = e_2 \min\left(1, \dfrac{(p - s_1y_1 - s_2y_2)/x}{s_2}\right) f_2(x)y_2 - d_2y_2. \end{cases} \tag{2.1}$$

Here, x, y_1 and y_2 are the densities of the prey and the two consumers respectively, r is the intrinsic growth rate of the prey (day^{-1}), d_1 and d_2 are the specific loss rates of the consumers that include respiration and death (day^{-1}). $f_1(x)$ and $f_2(x)$ are the consumers' ingestion rates, which are assumed to be bounded and smooth and also to satisfy

$$f_i(0) = 0, \quad f_i'(x) > 0 \quad \text{and} \quad \frac{f_i(x)}{x} \quad \text{is bounded for} \quad x \geq 0, i = 1, 2, \tag{2.2}$$

e_1 and e_2 are constant growth efficiencies (conversion rates or yield constants) for converting ingested prey biomass into consumer biomass. The second law of thermodynamics requires that e_1 and e_2 be < 1. k represents a constant carrying capacity that we relate to light in the following way: Suppose that we fix the light intensity at a certain value; then let the prey (which is a photo-autotroph) grow with no consumers but with ample nutrients. The prey density will increase until self-shading ultimately stabilizes it at some value, k. Thus, every k value corresponds to a specific limiting light intensity and we might model the influence of higher light intensity as having the effect of raising k; we assume that the prey's p (phosphorus):c (carbon) varies, but never falls below a minimum q (mg p/mg c); the two consumers maintain constant p:c ratios, s_1 and s_2 (mg p/mg c), respectively. More details about the biological background for (2.1) can be found in [1] and [2].

Let us assume that the average growth rates in system (2.1) change only at regular intervals of time. Then we can incorporate this aspect in system (2.1) and obtain the following modified system:

$$\begin{cases} \dfrac{1}{x(t)}\dfrac{\mathrm{d}x}{\mathrm{d}t} = r\left[1 - \dfrac{x([t])}{\min(k, (p - s_1y_1([t]) - s_2y_2([t]))/q)}\right] - \dfrac{f_1(x([t]))y_1([t])}{x([t])} - \dfrac{f_2(x([t]))y_2([t])}{x([t])}, \\ \dfrac{1}{y_1(t)}\dfrac{\mathrm{d}y_1(t)}{\mathrm{d}t} = e_1 \min\left(1, \dfrac{p - s_1y_1([t]) - s_2y_2([t])}{s_1x([t])}\right) f_1(x([t])) - d_1, \\ \dfrac{1}{y_2(t)}\dfrac{\mathrm{d}y_2(t)}{\mathrm{d}t} = e_2 \min\left(1, \dfrac{p - s_1y_1([t]) - s_2y_2([t])}{s_2x([t])}\right) f_2(x([t])) - d_2, \end{cases} \tag{2.3}$$

where $[t]$ denotes the integer part of $t \in (0, \infty)$. Systems of the type (2.3) are known as differential equations with piecewise constant arguments and these equations occupy a position midway between differential equations and difference equations.

By a solution of system (2.3), we mean a function $(x, y_1, y_2)^T$, which is defined for $t \in [0, \infty)$ and possesses the following properties:

1. x, y_1 and y_2 are continuous on $[0, \infty)$;
2. the derivatives $\frac{\mathrm{d}x(t)}{\mathrm{d}t}$, $\frac{\mathrm{d}y_1(t)}{\mathrm{d}t}$ and $\frac{\mathrm{d}y_2(t)}{\mathrm{d}t}$ exist at each point $t \in [0, \infty)$ with the possible exception of the points $t \in \{0, 1, 2, \ldots\}$, where left-sided derivatives exist;
3. the equations in (2.3) are satisfied on each interval $[n, n+1)$ with $n \in \mathbb{N} := \{0, 1, 2, \ldots\}$.

On any interval of the form $[n, n+1)$, $n = 0, 1, 2, \ldots$, we can integrate Eq. (2.3) and obtain for $n \leq t < n+1$,

$$\begin{cases} x(t) = x(n)\exp\left\{\left[r - \dfrac{rx(n)}{\min(k, (p - s_1y_1(n) - s_2y_2(n))/q)} - \dfrac{f_1(x(n))y_1(n)}{x(n)} - \dfrac{f_2(x(n))y_2(n)}{x(n)}\right](t-n)\right\}, \\ y_1(t) = y_1(n)\exp\left\{\left[e_1 \min\left(1, \dfrac{p - s_1y_1(n) - s_2y_2(n)}{s_1x(n)}\right) f_1(x(n)) - d_1\right](t-n)\right\}, \\ y_2(t) = y_2(n)\exp\left\{\left[e_2 \min\left(1, \dfrac{p - s_1y_1(n) - s_2y_2(n)}{s_2x(n)}\right) f_2(x(n)) - d_2\right](t-n)\right\}. \end{cases} \tag{2.4}$$

Letting $t \to n+1$, from system (2.4) we obtain

$$\begin{cases} x(n+1) = x(n)\exp\left\{r - \dfrac{rx(n)}{\min(k, (p - s_1y_1(n) - s_2y_2(n))/q)} - \dfrac{f_1(x(n))y_1(n)}{x(n)} - \dfrac{f_2(x(n))y_2(n)}{x(n)}\right\}, \\ y_1(n+1) = y_1(n)\exp\left\{e_1 \min\left(1, \dfrac{p - s_1y_1(n) - s_2y_2(n)}{s_1x(n)}\right) f_1(x(n)) - d_1\right\}, \\ y_2(n+1) = y_2(n)\exp\left\{e_2 \min\left(1, \dfrac{p - s_1y_1(n) - s_2y_2(n)}{s_2x(n)}\right) f_2(x(n)) - d_2\right\}, \end{cases} \tag{2.5}$$

for $n \in \mathbb{N}$, which is a discrete time analogue of system (2.1).

In the following sections, we will focus our attention on system (2.5). Throughout the rest of this paper, we consider only biologically meaningful initial values. Thus, we assume that $x(0) > 0$, $y_1(0) > 0$, $y_2(0) > 0$ and $y_1(0) + y_2(0) < p/s$, where $s = \max\{s_1, s_2\}$. And it is easy to check that the solution $(x(n), y_1(n), y_2(n))^T$ of system (2.5) is positive for all $n \in \mathbb{N}$.

3. Boundedness of solutions

In this section, we first establish the following boundedness result for system (2.5).

Theorem 3.1. *For system (2.5), assume that $f_i(x) \geq xh_i(x)$ and $h_i'(x) < 0\,(i = 1, 2)$ hold. Then we have for all $n > 0$,*

$$x(n) \leq \max\left\{x(0), \frac{w}{r}\exp(r-1)\right\} \equiv x_0, \qquad y_i(n) \leq \max\{y_i(0), v\}\exp(2e_if_i(x_0) - 2d_i) \equiv V_i,$$

where v is any number satisfying $e_if_i\left(x_0\exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)\right) < d_i$, $w = \min\left(k, \frac{p}{q}\right)$.

Proof. From system (2.5), we have

$$x(n+1) \leq x(n)\exp\left\{r - \frac{rx(n)}{\min(k, p/q)}\right\} = x(n)\exp\left\{r - \frac{rx(n)}{w}\right\} \leq \frac{w}{r}\exp(r-1) \equiv x^*.$$

Here we used the fact that $\max_{x\in R} x\exp\left(r - \frac{rx}{w}\right) = \frac{w}{r}\exp(r-1)$ for $r > 0$. Hence, for all nonnegative integers n, we have $x(n) \leq \max\{x(0), x^*\} \equiv x_0$.

If $e_if_i(x_0) \leq d_i$ $(i = 1, 2)$, then it is clear that for all $n > 0$, we have $y_i(n) \leq y_i(0)$. We thus assume below that $e_if_i(x_0) > d_i$. Let v be large enough that

$$f_i\left(x_0\exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)\right) < \frac{d_i}{e_i}.$$

We claim that for all nonnegative integers n, we have

$$y_i(n) \leq \max\{y_i(0), v\}\exp(2e_if_i(x_0) - 2d_i) \equiv V_i.$$

This is obviously true for $n = 1, 2$. In the following, we distinguish two cases to prove the claim.

Case (I): $y_i(0) \leq v$. If the claim is not true, then for some $n_1 > 2$, $v < y_i(n_1 - 2) \leq V_i$, $v < y_i(n_1 - 1) \leq V_i$, and $y_i(n_1) > V_i$. In this case, using the assumption that $h_i'(x) < 0$ and $f_i(x) \geq xh_i(x)$, $i = 1, 2$, we have

$$x(n_1 - 1) \leq x(n_1 - 2)\exp\left(r - \sum_{i=1}^{2} h_i(x(n_1 - 2))y_i(n_1 - 2)\right) < x_0\exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right).$$

This implies that

$$y_i(n_1) < y_i(n_1 - 1)\exp\left\{e_if_i\left(x_0\exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)\right) - d_i\right\} < y_i(n_1 - 1) \leq V_i,$$

which contradicts $y_i(n_1) > V_i$.

Case (II): $y_i(0) > v$. In this case, we have $x(1) < x_0 \exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)$. From (2.5), we can obtain $y_i(2) < y_i(1)$ $(i = 1, 2)$. In other words, as long as $y_i(n) > v$, we have $y_i(n+2) < y_i(n+1)$. Hence there are two possibilities: either (i) for some $y_i(n^*) \le v$ for some $n^* > 0$; or (ii) $y_i(n) > v$ for all $n > 0$. In case (ii), $y(n)$ is strictly decreasing for $n > 1$ and the claim is obviously true. In case (i), from the proof of case (I), we see that $y_i(n) < V_i$ for $n > n^*$ and hence the claim is also true. This completes the proof. ♯

From the above Theorem 3.1, we have

Corollary 3.2. *For system (2.5), assume $f_i(x) \ge x h_i(x)$ and $h_i'(x) < 0$ $(i = 1, 2)$ hold. Then the domain $\triangle \equiv \{(x, y_1, y_2) : 0 < x < \frac{w}{r}\exp(r-1), 0 < y_1, y_2 < v\}$ is globally attractive (here v is any number satisfying $e_i f_i\left(x_0 \exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)\right) < d_i$).*

Proof. In view of Theorem 3.1, it is easy to see that $\triangle$ is a positively invariant domain of system (2.5), and $x(n) \in (0, \frac{w}{r}\exp(r-1))$ for large values of n. Notice that if $y_i(n) > v$ for all $n > 0$, then $y_i(n)$ must have $y_i^* = \limsup_{n\to\infty} y_i(n) \ge v$ by boundedness. Hence for large values of n, we have

$$y_i(n) < y_i(n-1)\exp\left\{e_i f_i\left(x_0 \exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)\right) - d_i\right\}.$$

Letting $n \to \infty$ yields

$$y_i^* \le y_i^* \exp\left\{e_i f_i\left(x_0 \exp\left(r - \sum_{i=1}^{2} h_i(x_0)v\right)\right) - d_i\right\} < y_i^*.$$

This contradicts $y_i^* > v > 0$. Hence, the proof is complete. ♯

4. Global attractivity and numerical simulations

If $p - kq > 0$ and $s_1 y_1 + s_2 y_2 \le p - kq$, then we can obtain from (2.5) that

$$\begin{cases} x(n+1) = x(n)\exp\left\{r - \dfrac{rx(n)}{k} - \dfrac{f_1(x(n))y_1(n)}{x(n)} - \dfrac{f_2(x(n))y_2(n)}{x(n)}\right\}, \\ y_1(n+1) = y_1(n)\exp\left\{e_1 \min\left(1, \dfrac{p - s_1 y_1(n) - s_2 y_2(n)}{s_1 x(n)}\right) f_1(x(n)) - d_1\right\}, \\ y_2(n+1) = y_2(n)\exp\left\{e_2 \min\left(1, \dfrac{p - s_1 y_1(n) - s_2 y_2(n)}{s_2 x(n)}\right) f_2(x(n)) - d_2\right\}. \end{cases} \tag{4.1}$$

Note that all the parameters are the same as those in system (2.1).

Apart from the zero solution, system (4.1) always has $(x, y_1, y_2) = (k, 0, 0)$ as an equilibrium. In this section, we shall show that, under certain conditions, $(k, 0, 0)$ is globally attractive.

Theorem 4.1. *For system (4.1), assume that $e_i f_i(k) < d_i$. Then solutions of system (4.1) satisfy $x(n) \to k$, $y_1(n) \to 0$ and $y_2(n) \to 0$ as $n \to \infty$.*

Proof. Since $e_i f_i(k) < d_i$, there exists $\epsilon > 0$ such that $e_i f_i(k + \epsilon) < d_i$. Also, by the positivity of solutions and condition (2.2), we have

$$x(n+1) \le x(n)\exp\left[r\left(1 - \frac{x(n)}{k}\right)\right].$$

Therefore, we have $\limsup_{n\to\infty} x(n) \le k$, and there exists N_ϵ (positive integer) such that $x(n) < k + \epsilon$ for all $n \ge N_\epsilon$. Then, for $n \ge N_\epsilon$, we have

$$y_i(n+1) \le y_i(n)\exp[-d_i + e_i f_i(x(n))] < y_i(n)\exp[-d_i + e_i f_i(k+\epsilon)].$$

Since $e_i f_i(k + \epsilon) < d_i$, this implies that $y_i(n) \to 0$ as $n \to \infty$.

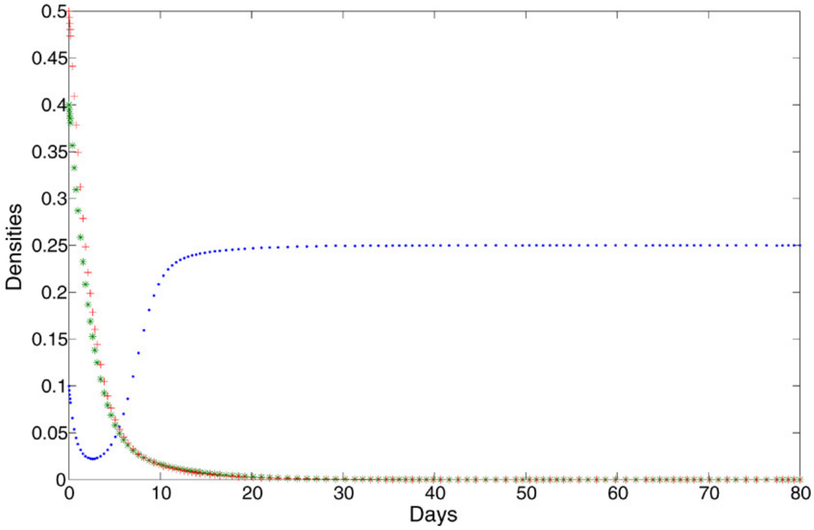

Fig. 1. $k = 0.25$.

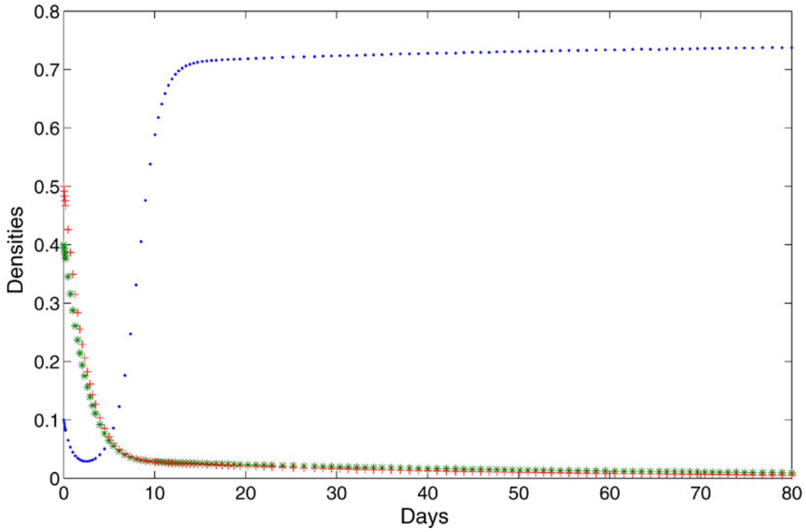

Fig. 2. $k = 0.75$.

Let $\eta \in (0, 1)$. Then there exists N_η (positive integer) such that, for $n \geq N_\eta$,

$$\frac{f_i(x(n))}{x(n)} y_i(n) < \eta \tag{4.2}$$

by the boundedness of $f_i(x(n))/x(n)$. Then, for $n \geq N_\eta$,

$$x(n+1) \geq x(n) \exp[r - r x(n)/k - 2\eta]. \tag{4.3}$$

Therefore, we have $\liminf_{n\to\infty} x(n) \geq k - 2\eta k/r$. Since $\eta \in (0, 1)$ was arbitrary, $\liminf_{n\to\infty} x(n) \geq k$. We already have $\limsup_{n\to\infty} x(n) \leq k$. Hence, $\lim_{n\to\infty} x(n) = k$.

The proof of the theorem is complete. $\sharp$

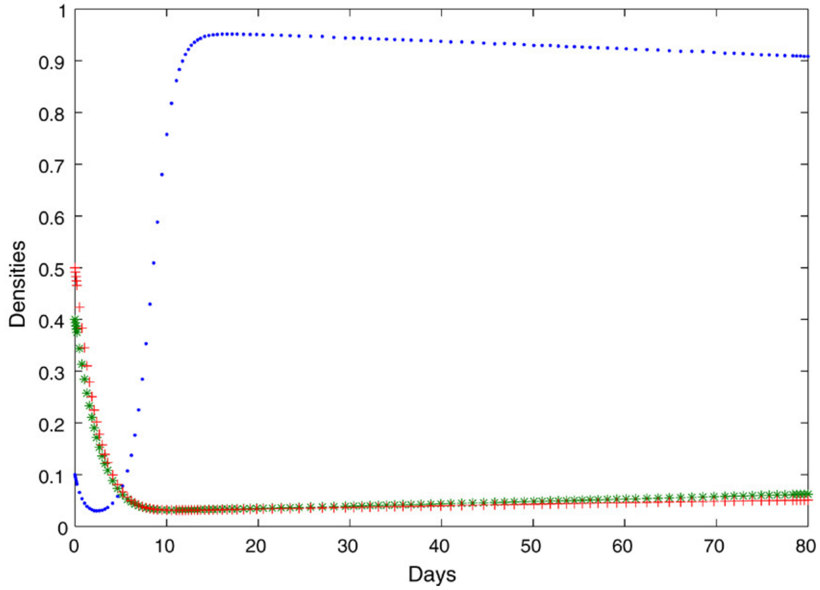

Fig. 3. $k = 1.0$.

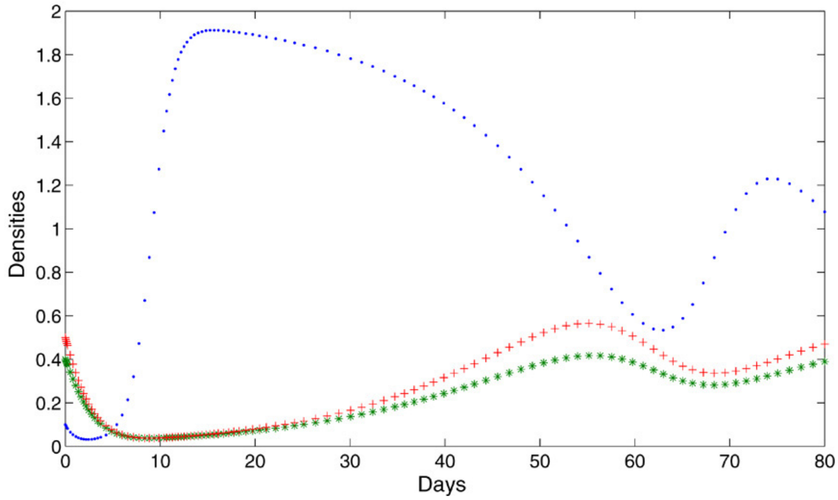

Fig. 4. $k = 2.0$.

Now we are ready to give some numerical simulations to illustrate our results. Consider the MacArthur–Rosenzweig type discrete model in [2]:

$$\begin{cases} x(n+1) = x(n)\exp\left\{r - \dfrac{rx(n)}{k} - \dfrac{f_1(x(n))y_1(n)}{x(n)} - \dfrac{f_2(x(n))y_2(n)}{x(n)}\right\}, \\ y_1(n+1) = y_1(n)\exp\{e_1 f_1(x(n)) - d_1\}, \\ y_2(n+1) = y_2(n)\exp\{e_2 f_2(x(n)) - d_2\}, \end{cases} \tag{4.4}$$

and we choose both $f_i(x)$ as Monod type functions:

$$f_i(x) = \frac{c_i x}{a_i + x}, \quad i = 1, 2.$$

Let the parameters be $r = 0.93$, $e_1 = 0.72$, $e_2 = 0.76$, $c_1 = 0.81$, $c_2 = 0.83$, $d_1 = 0.45$, $d_2 = 0.47$, $a_1 = 0.25$ and $a_2 = 0.30$. We will increase k from 0.25 to 2.0 in four numerical runs (see Figs. 1–4). We start with the same initial

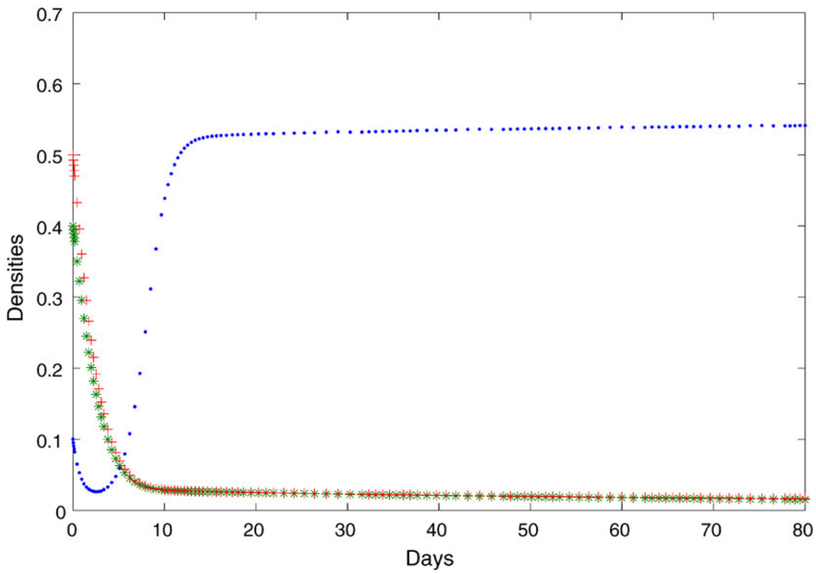

Fig. 5. $k = 0.56$.

conditions $x(0) = 0.1$, $y_1(0) = 0.4$, $y_2(0) = 0.5$ for all four runs. All of these parameters are biologically realistic (see [2]).

For $k = 0.4$ or $k = 0.75$, it is easy to verify that $e_i f_i(k) < d_i$. So the population densities are asymptotically stable around the equilibrium $(k, 0, 0)$. See Figs. 1 and 2.

For $k = 1.0$ or $k = 2.0$, it is also easy to verify that $e_i f_i(k) > d_i$. Figs. 3 and 4 indicate that the population densities are not attracted to the equilibrium $(k, 0, 0)$.

Now, let the parameters be $e_1 = 0.8$, $e_2 = 0.87$ and $k = 0.56$, with the others the same as above. Then $e_i f_i(k) = d_i$ holds. In this case, we can see that the population densities are also stable, around the equilibrium (0.56, 0, 0) (see Fig. 5).

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